

CYTOLOGICAL AND EVOLUTIONARY STUDIES ON PALUSTRES VIOLETS

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The genus *Viola* is well known for its many taxonomically difficult complexes. The classification is based on extensive studies carried out by different workers in Europe, North America, and Asia. However, more recent studies, specializing on smaller groups of the genus, have shown that re-evaluation of the classification is often necessary (Baker, 1949; 1953; 1957; 1960; Cain and Dansereau, 1952; Clausen, 1926; 1929; 1931; 1951; 1964; Russell, 1954; 1955; Russell and Crosswhite, 1963; Schmidt, 1961; Valentine, 1941; 1950). Within the four sections of the genus there are smaller subgroups which are in many cases connected together by hybrids only partially intersterile (Clausen, 1951). Within such subgroups a gradual chromosomal and morphological stabilization often takes place in a hybrid population, leading to introgressive establishment of several independent types, whose hybrid nature is often difficult to recognize without cytological or populational studies (Russell, 1954; Schöfer, 1954; Sorsa, 1965).

The *Palustres* group belonging to the subsection *Stolonosae* Kupffer, section *Plagiostigma* Godr. likewise presents taxonomic problems. No intensive cytological studies have hitherto been carried out on this circumpolar group of species as a whole (Clausen, 1964; Hulten, 1958).

The author had an opportunity of spending a year 1963–64 at the University of California, Berkeley, as an ASLA-Fulbright grantee. During that time herbarium material of the subsection *Stolonosae* was examined from the Herbarium of University of California, Berkeley, the Gray Herbarium, and the U.S. National Herbarium. Material for cytological studies was collected by the author on field trips from Alaska, Washington, Wyoming and California (see later for further explanation). Small flower buds were fixed in acetic-alcohol (3:1) either in the field or from plants grown first in the University of California Botanical Garden, Berkeley, and later at the Department of Genetics and the Botanical Garden of the University of Helsinki. The preparations were mostly made to catch PMC meiosis. Chasmogamous buds were preferred, because the anthers of the cleistogamous buds contain very few PMC's.

Excellent staining of squashes was obtained by the Feulgen method combined with post-staining with acetic-iron-hematoxylin adapted from Wittmann (1962).

The herbarium material of the species studied is deposited in the Botanical Museum, University of Helsinki, Finland.

THE PALUSTRES GROUP IN EUROPE

The central species of the Palustres group is *Viola epipsila* Led., which is a diploid $2n = 24$, $x = 12$ being considered to be the basic number of the section (Clausen, 1927; 1929; Löve and Löve, 1961; Sorsa, 1965). It hybridizes commonly in nature with its tetraploid counterpart *Viola palustris* L., which has the chromosome number $2n = 48$ (Clausen, 1927; 1929; 1964; Gershoy, 1932; 1934; Jørgensen et al., 1958; Löve and Löve, 1956; 1961; Schmidt, 1960; Sorsa, 1965), wherever their distribution overlaps in Fennoscandia, Northern Russia, and East Prussia (Hiitonen, 1934). It has been shown that the hybrids frequently resemble the *V. palustris* parent in morphological respects and can only be recognized as hybrids by cytological investigation or thorough analysis of a large population sample (Sorsa, 1965). The hybrid populations obviously mostly represent later hybrid generations and backcrosses with *V. palustris* (Sorsa, 1965).

VIOLA PALUSTRIS ssp. *JURESSII* (K. Wein.) Fourn. grows as disjunctive from *V. palustris* in France and Spain (Hulten, 1958), whereas both of the types are reported to occur in Britain (Clapham and Tutin, 1957). The taxonomic position of ssp. *juressii* has been uncertain: it has been reported as *V. epipsila* as well as a species in its own right, *V. juressii* Link. (Hulten, 1958). Its possible identity with the hybrid *V. epipsila* \times *palustris* has also been suspected (Eklund, 1958; Hiitonen, 1934). Morphologically, it is intermediate between *V. palustris* and *V. epipsila* (fig. 1). Fernandes (1950) reports the chromosome number $2n = 48$ from NE Portugal for *V. palustris* ssp. *herminii* Wein. This type may in fact be identical with *V. palustris* ssp. *juressii*.

Cytological investigations have now been carried out on plants of *V. palustris* ssp. *juressii* grown from seed which was obtained in 1962 from Portugal, near Ponte de Lima, through the kind offices of P. Silva and J. Jalas. The chromosome number proves to be the same as in *V. palustris*, $2n = 48$, and the meiosis is normal, showing 24 bivalents, all of about the same size (fig. 2). As far as the chromosomes are concerned, there thus seems to be no objection to granting this taxon sub-specific status as *V. palustris* ssp. *juressii*. Possibly the proper morphological species characters need reconsidering, which might result in merging ssp. *juressii* with *V. palustris*.

The *juressii* type is probably derived from the plants which were cut off in the south by the last Quaternary glaciation. It seems plausible that the tetraploid *palustris* had already spread to the new and more oceanic areas in Western Europe before the glacial period, while the diploid *epipsila* was more restricted to the continental and northern climate. The great glaciation thus left *Viola palustris* as disjunctive populations in the Central and South European mountain areas by restricting gene exchange with its more northern populations. Such a situation

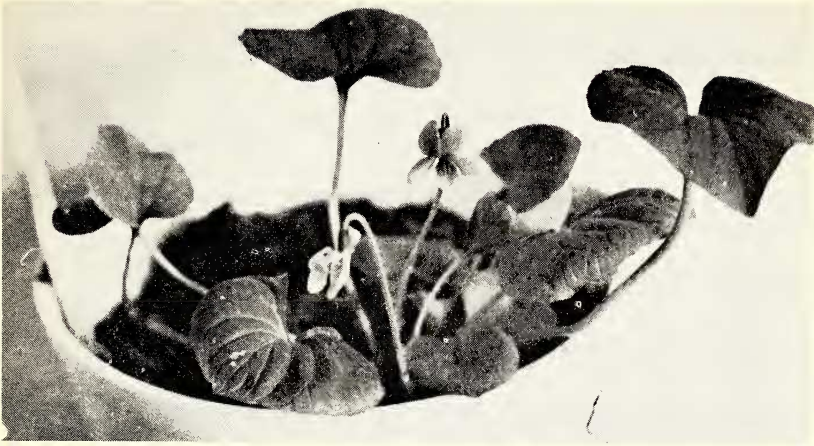


FIG. 1. *Viola palustris* ssp. *juressii*, an individual grown in greenhouse from seed obtained from Portugal; morphologically an intermediate between *V. palustris* and *V. epipsila*. It is tall (10–12 cm), having bluntly acute leaves, pubescent on the underside, and bracteoles above the middle of the pedicel. The flowers are of the same size and color as in *V. palustris*, only the spur being longer. In cultivation ssp. *juressii* is vigorous, spreading cleistogamously by seed and vegetatively by stolons.

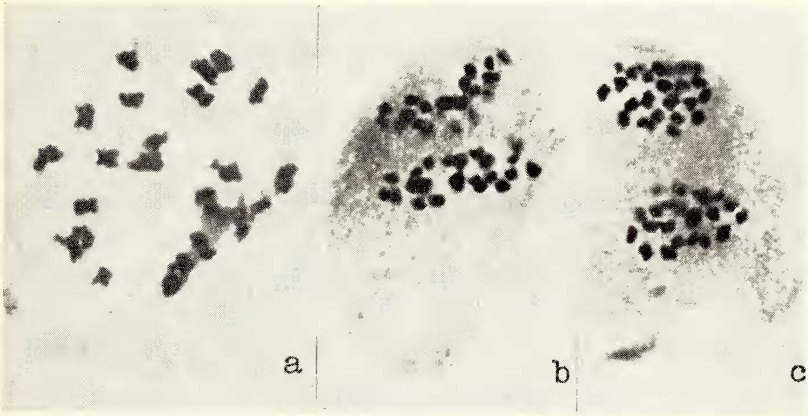


FIG. 2. PMC-meiosis in *V. palustris* ssp. *juressii*: a, Diakinesis showing 24 bivalents all about the same size; b, Anaphase I showing regular separation of paired chromosomes; c, Metaphase II showing $n = 24$ in both plates, \times ca. 1200.

would explain the slightly different morphological evolution of the southern isolates through genetic drift.

THE PALUSTRES GROUP IN NORTH AMERICA

Viola palustris has been used as a kind of general expression for Palustres violets in North America by many American taxonomists. Apart from wrong annotations on the herbarium specimens, *V. palustris*



FIG. 3. A plant of *Viola epipsila* ssp. *repens* from Moose Creek, Alaska; glabrous, acute leaves, larger flowers and smaller plant size (8–10 cm) than in *V. epipsila*.

is often confused with *V. epipsila* ssp. *repens*, *V. macloskeyi* ($n = 12$), *V. pallens* ($n = 12$), *V. renifolia* ($n = 12$), *V. incognita* ($n = 22$), or even *V. blanda* ($n = 22$), the North American *V. palustris* is by no means a uniform taxonomic entity.

Cytological investigations have now been carried out on four types belonging to the North American *palustris* complex as well as on one closely related member of the group.

VIOLA EPIPSILA Ledebour ssp. *REPENS* (Turczaninov) Becker, Bot. Centralbl. Beiheft 34(2): 406. 1917, has a wide distribution, from Eastern Asia to Alaska and western Canada. (Anderson, 1959; Hulten, 1947; 1958). It is reported from British Columbia and Washington (Hitchcock et al., 1961; Hämet-Ahti, 1965) but the specimens seen from that area differ slightly from the Alaskan type in morphological features. Moreover, the chromosomal condition seems to be quite different (see later for *V. palustris* in Washington).

Morphologically, the subspecies *repens* differs from the main type *V. epipsila* by a smaller size, glabrous but distinctly acute leaves, and larger flowers (fig. 3).

The chromosome number of the western subspecies has not been reported from North America (Clausen, 1964). However, in 1930 Miyaji determined the chromosome number $n = 12$ of a plant listed as *V. repens* Turcz. from the moors of Hokkaido. Obviously, this is the Japanese form of *V. epipsila* ssp. *repens*. The same chromosome number was now determined on specimens of three populations collected in Central Alaska, at Kantishna, Camp Denali and Moose Creek. The meiotic division is regular (fig. 4). No differences could be detected in chromo-

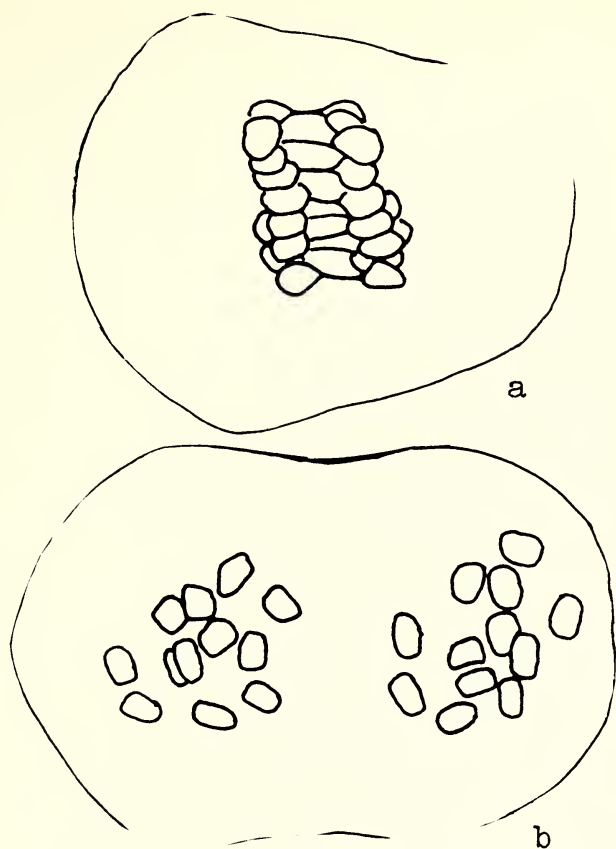


FIG. 4. PMC-meiosis of *V. epipsila* ssp. *repens* from Moose Creek, Alaska: a, Anaphase I showing regular separation of bivalent halves; b, Metaphase II showing $n = 12$ in both metaphase plates, \times ca. 1800.

some size or morphology between the Fennoscandian *V. epipsila* and the Alaskan ssp. *repens* (see Sorsa, 1965). The mitotic division accordingly showed $2n = 24$.

VIOLA ACHYROPHORA Greene, Pittonia 5: 33. 1902, has been reported from both continents in the Beringean area (Hulten, 1947; 1958), though not listed in the Flora of USSR (15:402-404. 1949). Hulten (1947) and Anderson (1959) were hesitant to rank this type as a separate species, merely because of slight morphological differences and a more northerly distribution. In the author's opinion, as well, the differences (smaller size, rounder and thicker leaves) between "*V. achyrophora*" and *V. epipsila* ssp. *repens* are mainly due to modification in the poorer and more northern habitats. No differences between the two are observable in style shape, either.

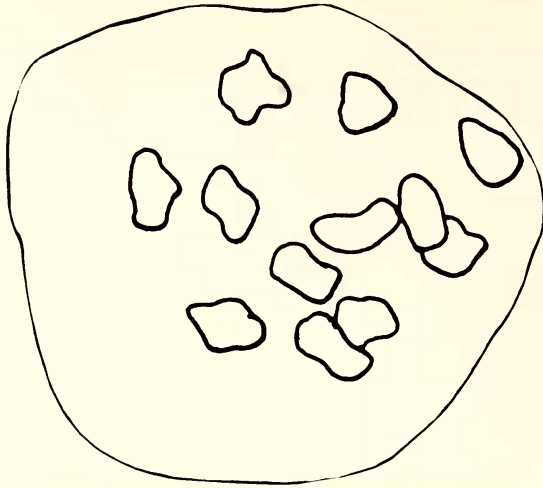


FIG. 5. PMC metaphase I of "*V. achyrophora*" from Chatanika River, Alaska, showing 12 normal bivalents all about the same size, \times ca. 1800.

The chromosomal picture of the *V. achyrophora* type is regular, showing 12 bivalents in meiosis, and no differences from *V. epipsila* ssp. *repens* can be noticed on the chromosome level (fig. 5). The same chromosome number has been found in both populations sampled north of Fairbanks, Alaska, namely Chatanika and Miller House.

It would seem more logical to regard "*V. achyrophora*" as just a northern variant of *V. epipsila* ssp. *repens* keeping it under the same specific name.

VIOLA PALUSTRIS Linnaeus, Sp. Pl. 934. 1753. As mentioned earlier, the name *V. palustris* has quite often been used as a general denomination for the whole *palustris* complex in North America. The author's acquaintance with the *palustris* type in the Eastern United States and Canada is restricted to herbarium material collected mostly around the turn of the century. Morphologically, this material is very near to the North European *V. palustris*, which is known also from Iceland, from where the chromosome number $2n = 48$ has been reported by Löve and Löve (1956), and Southern Greenland, from where $2n = 48$ has been confirmed by Jørgensen et al. (1958). In eastern North America the species occurs in New Foundland, Gaspé Peninsula, and Quebec on the Canadian side. From eastern U.S. it is reported around the White Mountain area only (Russell, 1965). However, no chromosome counts are available.

The *palustris* material seen from western North America, from British Columbia, Washington and the adjacent areas is morphologically quite near to what in Europe is considered the *epipsila* type (Hulten, 1958) in size, shape of leaves, flower characters and ecological requirements (fig. 6).



FIG. 6. Plants of the collective species of *Viola palustris* from Mt. Rainier Nat. Park, Washington. Morphologically this plant appears nearer the *epipsila* type: the flowers are large, pale blue, and have a long spur. Bracteoles are above the middle of the pedicel. Only two leaves are present at the time of flowering (*V. palustris* having three or more). Only the shape and glabrousness of the leaves resemble the *palustris* type.

Gershoy (1934) reported the chromosome number of $2n = 48$ from the Pacific coastal form of *V. palustris*, collected in the vicinity of Ocean Park, British Columbia. This plant was cytologically regular, having 24 bivalents in metaphase I. According to the morphological description of the plant given by Bold and Gershoy (1934) there are slight differences with the North European *palustris* e.g. in shape of leaves and color of seeds.

The herbarium specimens labelled as *V. palustris* from the Pacific coastal areas show a confusing variation of types not typical at all if compared with the North European *V. palustris*. Unfortunately no material was obtained of the Pacific coastal types in spite of several field trips to the sites of growth in California, given on the herbarium sheets (Humboldt Co., Mendocino Co.).

The writer has studied cytologically two types of the western *palustris* complex from Washington and Wyoming.

Plants belonging to the *Viola palustris* complex were fixed from an abundant population in Frog Heaven, Mt. Rainier National Park, Washington. Though the plants were morphologically more of the European *epipsila* type (fig. 6), they chromosomally belonged to the tetraploid level. The meiotic metaphase I showed minor irregularities in the first division (fig. 7). The meiotic picture very much resembles that of the previously studied *V. palustris* \times *epipsila* hybrids in Finland (Sorsa,



FIG. 7. Two PMC's in metaphase I of the *V. palustris* plant from Mt. Rainier Nat. Park, Washington. The orientation of the chromosomes is slightly irregular three small univalents (arrows) dividing not completely synchronous with the bivalent separation. $2n = 22-23_{II} + 2-3_{I}$, \times ca. 1200.

1965). Both seem to be well stabilized hybrid derivatives with little hybrid unbalance, the somatic chromosome number maintaining around $2n = 48$. The occurrence of the *epipsila* type characters in the tetraploid level such as the position of bracteoles and the number of leaves suggests the emerging of the *epipsila* genome. This can either be due to actual hybridization of the *palustris* type with the diploid *V. epipsila repens* taken place relatively recently. One can also think of the *epipsila* type as one of the progenitors of *palustris*, which would then lead into the emergence of various combinations of parental characters in different environments. It seems to me highly probable that some of the obscure western *palustris* types are of hybrid origin. The possible partners in the hybridization that obviously took place quite long ago will be discussed later.

VIOLA PALUSTRIS ssp. *BREVIPIES* Baker, Madroño 6: 235. 1936, has been described from several sites along the Colorado River at altitudes of 7500-10000 ft (Baker, 1936; probably also Russell, 1963). This white-flowered violet has obviously quite frequently been confused with *V. pallens* and *V. blanda*. The plant was found in July 1964 near Lewis Lake, Yellowstone National Park, Wyoming, though stated to be *V. blanda* in the local flora (McDougall and Bagglely, 1956). All characters, e.g. shape of style, beardless petals, size, shape of leaves and flowers (fig. 8) fit the description of Baker (1936) for ssp. *brevipes*.



FIG. 8. A plant of *Viola palustris* ssp. *brevipes* from Yellowstone Nat. Park, Wyoming. It has white flowers, a short spur, beardless petals, and has bracteoles above the middle of the pedicel. It is small, 5–8 cm, and the leaves are orbicular-cordate with regularly crenate margins.

The meiotic picture is suggestive of some hybridity in the population, revealed by somewhat irregular pairing and the presence of 2–5 univalents (fig. 9). Clausen (1964) also reports *V. palustris* ssp. *brevipes*, a type specimen from Colorado, Estes Park, as a hybrid derivative having “36–38 pairs or singles.” If about 12 are singles, the chromosome number might have arisen as a result of hybridization of a tetraploid and a d’plo:d counterpart. Clausen’s plant from Baker’s type collection possibly represents a young hybrid generation, in which chromosomal stabilization has not yet taken place. The Yellowstone population, in turn, may represent an older, balanced hybrid derivative, showing a rise of chromosome number and moderate stabilization, which is by no means uncommon among the violet hybrids (Brainerd, 1921; 1924; Clausen, 1922; 1926; 1931; Schmidt, 1961; Sorsa, 1965).

Without thorough experimental evidence one can only hazard a guess at the most probable history of this hybrid derivative. On morphological grounds (white flowers, round leaves, small size) the likeliest possibility would appear to be hybridization of the tetraploid western *palustris* type with the diploid *V. macloskeyi*, which occurs in similar habitats and areas. This continental and montane to subalpine form is possibly still evolving.

The chromosome number of *VIOLA MACLOSKEYI* Lloyd, *Erythea* 3: 74. 1895, was verified as $n = 12$ from specimens collected from four

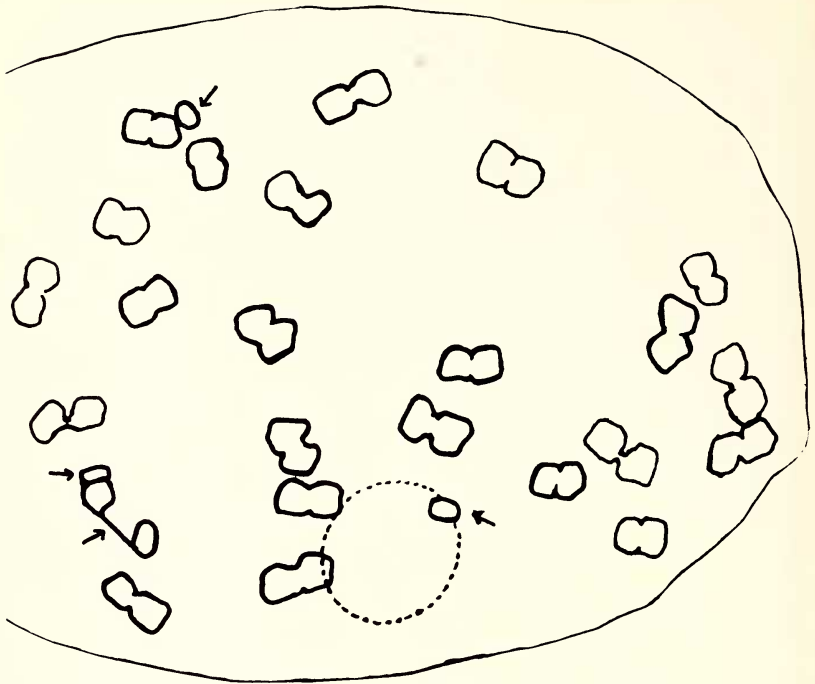


FIG. 9. Diakinesis of PMC meiosis in *V. palustris* ssp. *brevipetes* from Yellowstone Nat. Park, Wyoming; irregular pairing of the chromosomes, 24 bivalents (one loosely paired) and 3 fragments can be seen, \times ca. 1800.

populations, three from Yosemite National Park, California and one from a transplant No. 62.1302 in the Botanical Garden at Berkeley originally collected from Lake Tahoe (fig. 10). The same chromosome number has been reported earlier (Baker, 1953; Clausen, 1964).

REGIONAL AREAS OF SPECIES

The phylogenetic outlines of the genus *Viola* have been discussed most thoroughly by Clausen (1929). Although deductions of this type are always somewhat speculative, a combination of cytological, genetical and geographical information can provide some clue to what happened in the past. The Palustres group probably originated in north-eastern Asia, similarly to many circumpolar groups of species. The diploid level is represented as *Viola epipsila*, and the tetraploid as *V. palustris*. The ready hybridization of the two suggests that the origin of the tetraploid *palustris* was probably through hybridization of two diploid types, one of which was the *epipsila* type (fig. 11).

The tetraploid type has expanded its range into more oceanic environments, while the diploid *epipsila* type covers the more continental areas of Northern Europe, and as a slightly differentiated subspecies

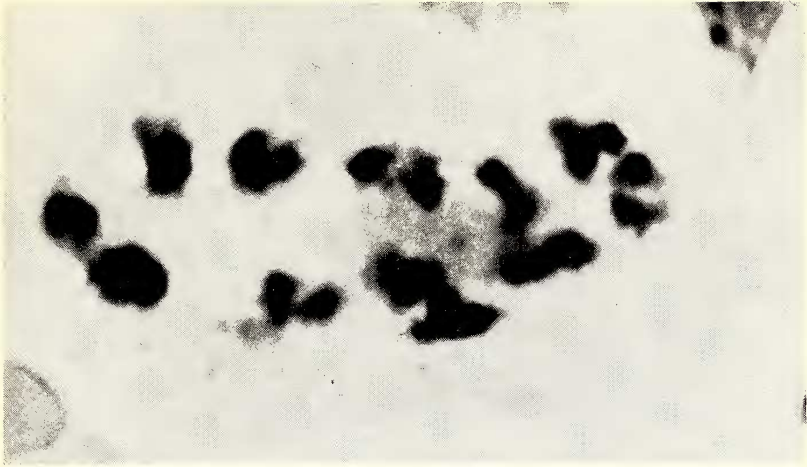


FIG. 10. Diakinesis of PMC meiosis in *Viola macloskeyi* grown in Botanical Garden, Berkeley (No. 62.1302); $n = 12$, the bivalents appear to be mostly ring-shaped, which was found to be frequent in all the *macloskeyi* samples studied, \times ca. 1200.

repens extends to Siberia and the Beringean area as far as Alaska and possibly western Canada. The tetraploid *palustris* type is widespread in Europe and is connected to Eastern North America over Faeroe Islands, Iceland and Greenland. In North America it tends to have a bi-coastal distribution, although the author is inclined to believe that the original "Linnean" species *V. palustris* is confined to the eastern coast, i.e. Newfoundland and Gaspé Peninsula in northeastern Canada, and the White Mountains area in the United States, while the western types of *palustris* are less typical and often show variation in character combinations.

It seems probable that much of the variation of the *palustris* type is caused by hybridization with ecologically and karyologically suitable related violets, such as species of the diploid group ($n = 12$) *V. macloskeyi*, *V. pallens* and possibly also *V. lanceolata*, *V. primulifolia* and *V. renifolia*. Evidence from the extensive crossing experiments of Gershoy and his co-workers (Bold and Gershoy, 1934; Gershoy, 1934) drops out the more distant relatives of the Palustres group such as *V. blanda* and *V. incognita* (both $n = 22$) and *V. selkirkii* ($n = 12$). The possibility of hybridization between the eastern *palustris* with the northwestern *epipsila repens* cannot be excluded, either.

The cluster of species forming the Palustres group thus seems to consist of one tetraploid, *V. palustris*, and at least three diploids, namely *V. epipsila* and the species pair *V. macloskeyi*-*V. pallens*. Experimental evidence is needed to confirm their evolutionary possibilities in creating the variety of forms that constitute the taxonomically difficult Palustres group.

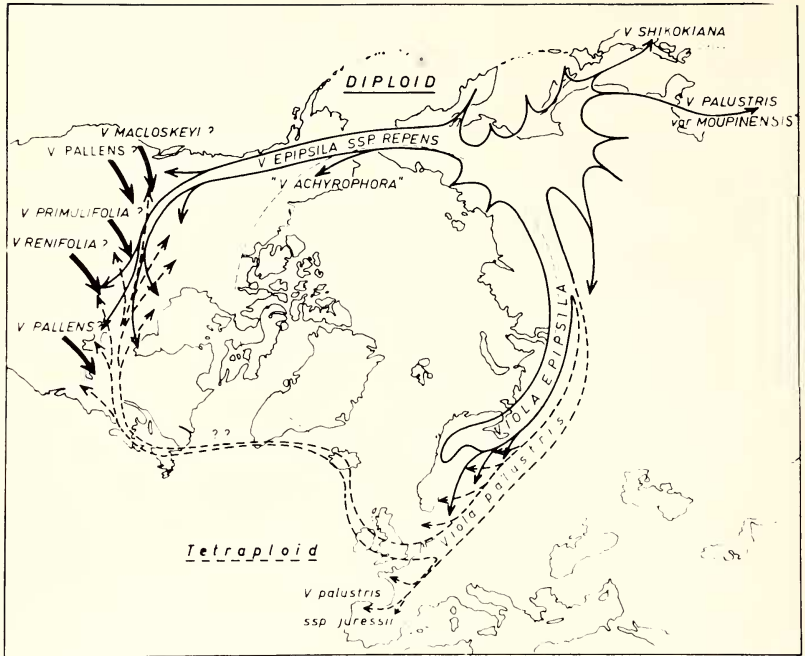


FIG. 11. Schematic representation of the speculative evolutionary outlines in the Palustres group. The full lines represent diploid species, the broken lines tetraploid species. Heavy arrows in North America suggest the possible contributors to the variability of the *palustris* complex. *V. shikokiana* ($n=12$, Miyaji, 1929) is the East Asiatic counterpart of the *macloskeyi-pallens* species pair, *V. palustris* var. *moupinensis* is probably a separate species reported from Southern China. See further in the text.

ACKNOWLEDGMENTS

I wish to express my sincere gratitude to the great authority on the genus *Viola*, Jens Clausen, Carnegie Institution of Washington, Stanford, for reading the manuscript and making numerous valuable comments both to amend the factual information and to improve my English text. I also want to thank Esko Suomalainen, University of Helsinki, Finland, for advice and encouragement during the studies, and Jaakko Jalas, University of Helsinki for help and criticism during the work. Herbert G. Baker, Margaret Bergsens and Annetta Carter, University of California, Berkeley, were always kindly helping me in many ways during my stay at Berkeley.

The field trip to Alaska in June 1964 was sponsored by U.S. Government Grant No. 33511-215009 given to me by the International Institute of Education.

SUMMARY

Chromosome numbers of violets belonging to the Palustres group, subsection *Stolonosae* Kupff. are reported:

Viola palustris ssp. *juressii* (K. Wein.) Fourn. $n = 24$, from cultivated plants grown from seed obtained from Portugal, near Ponte de Lima. Meiosis normal.

Viola epipsila ssp. *repens* (Turcz.) Becker, $n = 12$, from three different localities in Central Alaska (Kantishna, Camp Denali, Moose Creek). Meiosis normal.

"*Viola achyrophora*" Greene, $n = 12$, from two localities in Northern Alaska (Chatanika, Miller House). Meiosis normal. It is suggested that this type should be treated rather as belonging to *V. epipsila* ssp. *repens*.

Viola palustris (coll.), $n = 22-23_{II} + 2-3_I$, slightly irregular meiosis, from Frog Heaven, Mt. Rainier National Park, Washington. The type obviously represents a stabilized hybrid derivative probably quite frequent among the North American *palustris* complex.

Viola palustris ssp. *brevipes* Baker, $n = 22-24_{II} + 3-5_I$, slightly irregular meiosis, from Lewis Lake, Yellowstone National Park, Wyoming, represents a type of stabilized hybrid derivative. The most probable progenitors are the western *palustris* type and the white-flowered diploid *V. macloskeyi*.

Viola macloskeyi Lloyd (= *V. macloskeyi* ssp. *macloskeyi* Baker), $n = 12$, normal meiosis, from a Lake Tahoe transplant and three sites in Yosemite National Park, Calif.

The emergence of some key morphological characters of *V. epipsila* on the tetraploid level in *V. palustris* ssp. *juressii* and especially in the western North American *V. palustris* has been observed and discussed.

The distribution of the diploid and the tetraploid types of the Palustres group has been presented. The group seems to consist of an evolutionary active complex, able to balance itself in different environments by forming various types due to selection and genetic drift.

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A SECOND SPECIES OF AMMOBROMA (LENNOACEAE), IN SINALOA, MEXICO

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The genus *Ammobroma* has stood as a monotypic taxon since its initial description more than a hundred years ago (Gray, 1854). Its single species, *A. sonorae*, has through the years attracted much casual attention because of the curious, mushroom-like appearance of the plant, and because of its early use as an edible plant by some of the indigenous Indian tribes of the Sonoran region. It is of some interest to note that Dr. Jerry Rzedowski has observed the use of *Lennoa* also as a vegetable in the State of San Luis Potosí (personal communication). Notwithstanding the obvious interest in these bizarre parasites very little botanical work has been done in the family.

It is not our intention here to enter into a discussion of the generic distinctions between the three known genera of Lennoaceae (*Ammobroma*, *Pholisma*, and *Lennoa*). Even a casual acquaintance with *Pholisma* and *Lennoa* leaves one with an uneasy feeling about their validity as genera. It could even be argued that the main generic feature of *Ammobroma*, i.e., the compact, laterally extended head, is insufficient by itself as a generic distinction.

Whatever generic delimitations may be used in the future, it is of great interest that we can now add a new species to this small family. At present the species must undoubtedly be placed in *Ammobroma*. The plant was first observed by the senior author in December, 1949, in the region of Culiacán, Sinaloa. Only dried and decomposed remains were found at that time. It could be ascertained, nevertheless, that the plants were attached to the roots of *Euphorbia (Agaloma) californica*. More recently (August, 1957), a second visit was made to the same locality, and many flowering plants were found on the roots of *Euphorbia californica*, *Jatropha curcas*, and *J. cordata*. As now known, the parasite is